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Biomass production, N:P ratio and nutrient limitation in a Caucasian alpine tundra plant community

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Abstract

Questions: 1. To what extent is biomass production of a Caucasian alpine tundra plant community limited by soil nitrogen and/or phosphorus? 2. Can the foliar N:P ratio predict the nutrient limitation pattern of alpine vascular plant communities?

Location: Lichen-rich tundra on Mt. Malaya Khatipara in the NW Caucasus, Russia (43°27' N, 41°42' E; alt. 2800 m a.s.l.).

Methods: We conducted a 4-year fertilization experiment (N, P, N+P, lime additions and irrigation) on the alpine tundra in the northwestern Caucasus, Russia. We determined responses of biomass, tissue nutrient concentrations and nutrient pools of the above-ground component of the plant community.

Results: Total plant community biomass did not respond to fertilization. However, lichen biomass strongly decreased in response to the N- and N+P treatments, whereas vascular plant biomass increased in response to the N- and even more to the N+P treatment, but not to P or lime addition or irrigation. P-concentrations in vascular plant species were very low, but their biomass production was not principally P-limited, suggesting adaptation to low soil P-availability. The N-limitation of vascular plant biomass production in the community, which in lowlands usually occurs at N:P ratios below 16, could not be predicted from the mean foliar N:P mass ratio in the control (N:P = 29).

Conclusions: This Caucasian alpine plant community is an example of N- and P-co-limitation of vascular plant biomass production, with N being the principal and P the secondary limiting nutrient. Critical N:P ratios as determined for lowland communities are not applicable here.

Keywords: Alpine lichen grassland; Fertilization; Leaf nutrient concentration; Nitrogen; Phosphorus; Productivity.

Nomenclature: Vorob'eva & Onipchenko (2001).

Introduction

Biomass productivity of alpine tundra communities is low compared to that of other ecosystems (Bowman & Fisk 2001), probably because of nutrient limitation to plant growth. Körner (2003) suggested that, due to the low nitrogen mineralization rate and relatively high phosphorus availability caused by weathering, most alpine communities are nitrogen-limited. Indeed, Bowman et al. (1993) demonstrated nitrogen limitation of alpine tundra plant communities in the Colorado Rocky Mountains. However, generalizations would be premature since only few mountain ecosystems have been experimentally studied for nutrient limitation related to biomass production. The former Soviet Union includes a substantial part of the world's mountain areas, yet despite some research published mostly in Russian (e.g. Shatvorjan 1960; Nakhutsrishvili 1976; Khutinaev 1981) the mineral nutrition of its alpine plant communities remains largely unexplored.

A popular research method to define nutrient limitation of a plant community has been to measure the biomass response to experimental fertilization, mostly N- and P-additions. However, this method is laborious, costly and sometimes there are difficulties in the interpretation of the results (Aerts & Chapin 2000). Koerselman & Meuleman (1996) proposed the above-ground biomass N:P ratio as a quantitative tool to assess the nutrient limitation of wetland plant communities, where ratios below 14 indicated N-limitation, ratios higher than 16 indicated P-limitation and ratios between 14 and 16 possible N- and P-co-limitation. Several authors have since reported a similar relation between N:P mass ratios and the type of nutrient limitation for wetland plant communities (Güsewell et al. 2003; Olde Venterink et al. 2003).

Despite this, the generality of the Koerselman & Meuleman model is still debated. Tessier & Raynal (2003) found considerable variability between plant communities in N:P ratio thresholds for N- versus P-limitation. Bowman et al. (2003) found no correlation between foliar N- or P-concentrations in three widespread alpine species and soil N- or P-supply. Körner (1989) suggested that herbaceous plants at higher altitudes have higher N- and P-concentrations than those of similar species at lower elevations, owing to "inherent developmental growth constraints inhibiting nutrient dilution in the plant body". Thus, the N:P ratio threshold for high altitude ecosystems might differ from that of lowland ecosystems. However, little information is available about critical N:P ratios of mountain plant communities (Tessier & Raynal 2003),

especially for lower latitudes.

Here we explore type and degree of nutrient limitation of Caucasian alpine tundra addressing five questions:

1. Which nutrients limit the above-ground biomass production of this alpine tundra plant community?
2. Can this limitation be predicted from the community N: P mass ratio?
3. Is the pattern of response to nutrient addition the same for the whole community as for its component species?
4. How do the main component vascular species respond to release from nutrient limitation in terms of biomass production and nutrient uptake?
5. How do the relative contributions of these species in the total above-ground N- and P-pools change with nutrient addition?

To answer these questions we performed a 4-year fertilization and irrigation experiment in a Caucasian alpine lichen-rich tundra and examined the responses in biomass and N- and P-content of the different species.

Methods

Site description

The experimental site was in the Teberda Natural Reserve (43°27' N, 41°42' E), on the south wind-exposed slope of Mt. Malaya Khatipara (at 2800 m a.s.l.), in the NW Caucasus, Russia. Soils of the site are Umbric Leptosols (FAO Classification System) with many stones, mostly biotite shists. The upper soil horizon is acidic (pH_{KCL} = 4.0) and nutrient-poor (available NH_4 = 0.0012 %, available P = 0.0006%) (Onipchenko 1994).

The climate of the area is rather harsh, with a mean annual temperature of 1.2 °C and a mean July temperature of 7.9 °C (Grishina et al. 1986). Annual precipitation is high (1400 mm), but most falls as snow and is blown away due to high wind velocities. Therefore, summer soil water shortage and deep winter freezing occur frequently. The vegetation season lasts from about mid May to September. Senescence starts around the first week of September in most vascular plants.

About 50% of the soil area is covered by fruticose lichens, mainly *Cetraria islandica*. Vascular plants create 10-20 cm diameter patches alternating with similarly sized lichen patches. There are no clear dominant species among the vascular plants. The most abundant species are graminoids: *Festuca ovina, Carex sempervirens*, *Carex umbrosa*; forbs: *Alchemilla caucasica*, *Anemone speciosa*, *Antennaria dioica*, *Trifolium polyphyllum*; and the dwarf shrub *Vaccinium vitis-idaea*. Our plant community is an 'alpine lichen heath' *sensu* Wielgolaski (1972). For a detailed description see Onipchenko (1994, 2002).

Experimental treatments and sampling

The experiment covered the period May 1999 – August 2002. We assigned 24 plots of 1.5 m × 1.5 m, visually similar in plant species composition, to six treatments: (1) control, (2) nitrogen (N), (3) phosphorus (P), and (4) N+P fertilization, with nutrients added annually just after snow melt, (5) lime ($CaCO_3$) addition just after snow melt in 1999 and 2002, and (6) irrigation conducted annually during the main vegetation period (July - August). Each treatment was replicated 4 times. Spatially randomized plots were deployed in three rows perpendicular to the slope, eight plots per row, with a 1 m buffer zone between plots within as well as between rows. Nitrogen was added as urea (9 g-N.m^{-2}.a^{-1}), phosphorus as double superphosphate (2.5 g-P.m^{-2}.a^{-1}), and lime added at 52 g.m^{-2}.a^{-1}. The lime treatment was aimed at lowering soil acidity, which could affect N- and P-availability (Rorison 1980). Irrigation was aimed at overcoming possible summer soil water constraints. Every day the precipitation was measured and if the precipitation over a 3-day period did not compensate for water loss due to evapotranspiration (about 3 mm per day; Grishina et al. 1986), the plots were irrigated accordingly.

Total above-ground biomass (including both lichens and vascular plants) was sampled in summer 2002 during the first week of August, at the peak of the growing season of this relatively late and cold summer. In each plot two 0.25 m × 0.25 m subplots were cut close to the soil surface. Lichens were not sorted by species, but the harvested vascular plant material of both subplots was bulked and sorted by species. Vegetative parts and flowering stems were separated, air-dried then oven-dried (60 °C) and weighed. The three morphologically similar *Carex* species (*Carex umbrosa*, *Carex sempervirens* and *Carex caryophyllea*) were pooled as *Carex* spp. Ten representative species, which constituted about 80 % of total vascular species community biomass, were selected for chemical analyses: nine forbs (see Fig. 2) and *Vaccinium vitis-idaea*. Only leaves (with petioles if any) were analysed for N and P. N-concentrations were determined by dry combustion on a Perkin Elmer 2400 CHNS analyser. For determination of P-concentrations, samples were acid digested and analysed colorimetrically using the ammonium molybdate method (Murphy & Riley 1962). In order to find out whether the lime treatment affected soil acidity we sampled soil from control and lime fertilized plots. These samples were sieved and analysed for pH-KCl and total acidity, the latter after titration with NaOH.

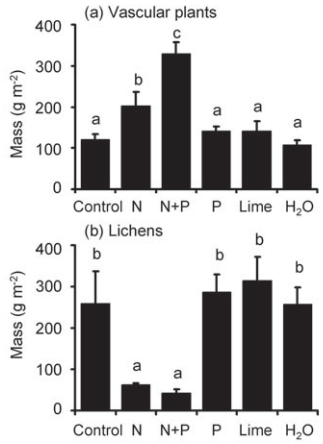

Fig. 1. Above-ground biomass ($g.m^{-2}$) response to experimental treatments. N: annual nitrogen addition (9 $g\text{-}N.m^{-2}.a^{-1}$), P: annual phosphorus addition (2.5 $g\text{-}P.m^{-2}.a^{-1}$); N+P: annual addition of nitrogen and phosphorus together (9 $g\text{-}N.m^{-2}.a^{-1}$ + 2.5 $g\text{-}P.m^{-2}.a^{-1}$), Lime: lime addition in first and final year of the experiment (52 $g\text{-}lime.m^{-2}.a^{-1}$); H_2O: annual irrigation during July and August. **a.** vascular plants; **b.** lichens. Error bars represent SE ($n = 4$). Different letters indicate significant difference among treatments ($p < 0.05$, post-hoc Tukey test following one-way ANOVA).

Statistical analysis

First the responses of lichen biomass, total above-ground vascular plant biomass and above-ground biomass of individual species were analysed by one-way ANOVAs followed by the Tukey HSD post-hoc test. The N+P-treatment was considered as a single factor treatment in this analysis. As lime additions and irrigation did not have any significant effects (see Results) we tested for N- and P-interactions in two-way ANOVAs, with lichen biomass, vascular plant biomass or biomass of individual vascular species as dependent variables and N- and P-addition as independent ones. Where necessary, logarithmic transformation was applied to improve normality. In order to compare individual treatment means, we did additional one-way ANOVAs followed by a Tukey post-hoc test, for biomass and leaf nutrient concentrations.

The total amount of N and P in the vegetative parts of each species per plot was calculated by multiplying vegetative biomass per m^2 by leaf N- or P-concentration for each species. As all analysed herbaceous species formed rosettes or tufts we assumed that the N- and P-pools in vegetative stems were negligible compared to those in leaves. However, flowering stems of other species and woody biomass of *Vaccinium vitis-idaea* may differ in their nutrient concentrations. Therefore, we only used vegetative biomass for these analyses and excluded *V. vitis-idaea*. These data, log-transformed where necessary, were subjected to three-way ANOVAs with N- and P-additions and species as independent variables, and species N- or P-content as a dependent variable. Owing to significant species effects, separate two-way ANOVAs were done with N and P as independent variables and species mean above-ground N- and P-pools as dependent variables.

The soil pH in control plots was compared to that in limed plots using a *t*-test.

Results

Despite an overall treatment effect ($p < 0.001$) on above-ground vascular plant biomass and lichen biomass (Fig. 1), we did not find any significant response to lime additions nor to irrigation, even though we found a higher soil pH-KCl after lime treatment (4.7 ± 0.05 in control and 5.2 ± 0.2 in limed plots, $p = 0.013$). Neither did we find significant responses to these treatments in the above-ground biomass of individual species or in species nutrient content (data not shown). Therefore, we confine ourselves hereafter to changes induced by N- and/or P-fertilization.

Biomass responses

The total community biomass (lichens and vascular plants) did not change significantly in response to treatments. However, we observed a strong biomass shift from lichens to vascular plants. In the controls the above-ground vascular plant biomass was relatively low at about $120\ g.m^{-2}$, but almost doubled in response to N-fertilization and almost trebled in response to the N+P-treatment, while there was no response to the P-treatment. In contrast, lichen biomass, as high as $260\ g.m^{-2}$ in the controls, was reduced to 60 and 40 $g.m^{-2}$ in response to N- and N+P-fertilization. Although the lichen biomass response to N- and N+P-treatments differed, there was no significant interaction between N- and P-fertilization. In contrast, there was a significant interaction between the N- and P-treatments for vascular plants (N treatment: $p < 0.001$; P-treatment: $p = 0.009$; $N \times P$: $p = 0.042$). Thus, P-addition caused a change in above-ground vascular plant biomass only in combination with N-addition (Fig. 1a).

The response of above-ground biomass or foliar N- and P-concentrations of species to the treatments varied and showed no clear-cut pattern (see App. 1). None of the species excluded from nutrient content analyses had any significant biomass response (data not shown).

Leaf N- and P-concentrations and pools

The foliar N:P ratio of the controls varied substantially among species (Table 1). The pooled vascular

Table 1. Species N:P ratios in control plots and mean percentage (± SE, $n = 4$) of the individual species contributions to the total above-ground nitrogen and phosphorus pools.

Plant variable	N:P	Nitrogen pool				Phosphorus pool			
Experimental treatment		control	N	N+P	P	control	N	N+P	P
Species									
Alchemilla caucasica	67	3.1 ± 2.1	2.3 ± 1.7	12.2 ± 5.4	1.1 ± 0.5	1.4 ± 0.9	0.9 ± 0.7	10.4 ± 4.6	1.2 ± 0.5
Anemone speciosa	19	8.0 ± 2.7	5.0 ± 1.6	5.9 ± 3.1	10.8 ± 1.8	12.1 ± 4.1	7.8 ± 2.5	4.8 ± 2.5	7.5 ± 1.3
Antennaria dioica	21	4.7 ± 1.7	9.9 ± 5.6	6.2 ± 2.8	15.0 ± 8.7	6.2 ± 2.3	18.2 ± 10.3	8.6 ± 3.9	21.4 ± 12.4
Campanula tridentata	21	10.7 ± 2.8	3.0 ± 0.7	3.4 ± 1.3	9.1 ± 2.6	14.6 ± 3.9	3.8 ± 0.9	3.8 ± 1.4	7.3 ± 2.1
Carex spp.	39	18.1 ± 2.9	41.2 ± 10.1	27.6 ± 10.7	7.8 ± 1.6	13.3 ± 2.1	29.2 ± 7.2	23.4 ± 9.0	10.2 ± 2.1
Carum caucasicum	21	8.7 ± 1.8	4.1 ± 1.7	3.6 ± 1.9	1.8 ± 0.9	12.9 ± 2.7	6.0 ± 2.5	5.5 ± 2.9	2.9 ± 1.4
Festuca ovina	59	22.4 ± 4.3	8.9 ± 2.0	35.1 ± 3.9	28.1 ± 2.7	11.6 ± 2.2	1.1 ± 0.2	39.3 ± 4.4	35.8 ± 3.4
Pedicularis comosa	12	0.2 ± 0.2	2.1 ± 1.0	0.6 ± 0.6	0.4 ± 0.3	0.5 ± 0.5	1.8 ± 0.9	1.1 ± 1.1	1.2 ± 0.7
Trifolium polyphyllum	25	24.0 ± 8.4	23.5 ± 15.4	5.2 ± 5.0	25.9 ± 7.2	27.5 ± 9.7	31.3 ± 20.5	3.3 ± 3.2	12.5 ± 3.5

plant foliar N:P mass ratio in the control was 29. The leaf concentration of N in the controls varied from 12.1 to 42.8 mg.g^{-1} dw. The N-addition treatments (N and N+P) increased the N-concentration of above-ground plant tissue for all species (although not in all cases significantly). The increase in N induced by the N-treatment tended to be consistently higher than that caused by the N+P-treatment. Similarly, the phosphorus addition treatments (P and N+P) increased the P-concentration of above-ground plant tissue for all species and this increase caused by the P-treatment tended to be higher than in the N+P-treatment.

Considering that the analysed species accounted for 80% of the total vascular species biomass, we estimate the mean total amount of N in the control at 1.5 g.m^{-2} and of P at 0.05 g.m^{-2}. By the end of the experiment the total above-ground vascular plant N-pool in the N-plots had increased 2.8-fold and in the N+P plots 3.2-fold. Thus, out of 36 g of added N, only 2.6 g had been taken up by the above-ground vegetation in the N-plots and 3.2 g in N+P-plots. The total above-ground vascular plant P-pool increased 8.3-fold in the P-plots and 13.2-fold in the N+P-plots. Thus, out of 10 g P added, 0.3 g and 0.54 g of P had been taken up by vascular plants in the P- and N+P-plots, respectively.

The three-way ANOVA on the total N-pool showed a significant overall effect of N ($p < 0.001$), and significant N × species ($p < 0.001$), P × species ($p = 0.005$) and N × P × species ($p = 0.013$) interactions (see also Fig. 2). The three-way ANOVA on P-pool showed significant overall effects of P-additions ($p < 0.001$), N-additions ($p = 0.002$), and significant P × species ($p < 0.001$), N × species (0.019) and N × P × species ($p = 0.007$) interactions.

Although the total nitrogen contents of all nine species combined were similar in the N- and N+P-treatments, the distribution of N over the species was very different (Fig. 2). Remarkably, the N-content was significantly different only for three individual species, while P-content was significantly different for eight species out of nine. Consequently, the relative contributions of individual species to the total nitrogen and phosphorus pools were also strongly influenced by the treatments (Table 1).

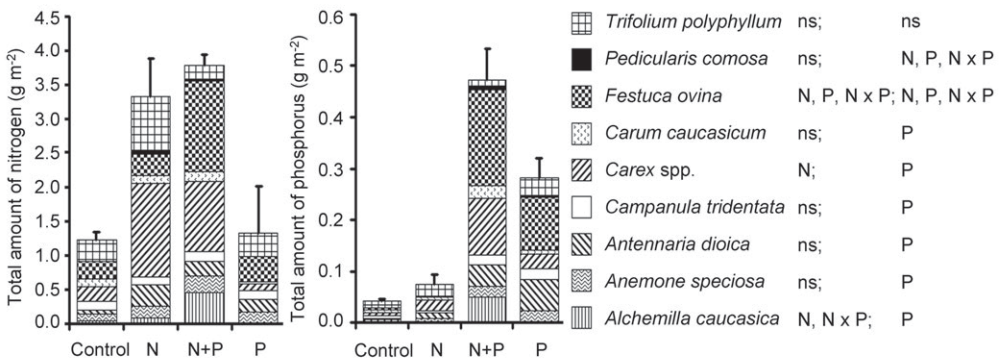

Fig. 2. Distribution of mean above-ground vascular plant N- and P-pools among species at different treatments (for treatment description see Fig. 1). Error bars represent SE ($n = 4$) of the total N- or P-pool. Significance of response to N- and P-additions and their interaction (based on two-way ANOVA) is indicated first for the N-pool, and after the semicolon for the P pool. $p < 0.05$; ns = not significant.

Discussion

Nutrient limitation and N:P ratio of the vascular plant community

The lack of any response to irrigation and lime additions suggests that the community nutrient limitation is not a result of water shortage or low soil pH but rather of low soil nutrients *per se*. Our results for the alpine tundra in the Caucasus support Körner's (2003) hypothesis that vascular plant biomass production in alpine plant communities is mostly nitrogen-limited. In agreement with Liebig's law of the minimum (von Liebig 1840) P-additions did not change the vascular plant community biomass production until the N-limitation was overcome. Thus, only when applied together with N- and P-addition increased the vascular plant biomass significantly (Fig. 1).

Consistent with previous findings (e.g. Press et al. 1998; Tomassen et al. 2004), lichens responded negatively to N-containing fertilizers. Our analyses can not distinguish whether this decrease is a result of shading by the expanded canopy of vascular plants (Cornelissen et al. 2001) or a direct damaging effect of urea, which may cause tissue burning (Bremner 1995).

We found relatively low mean N- and, especially, P-concentrations in leaf tissue (1.7% and 0.06%, respectively) compared to those found previously (Wielgolaski et al. 1975; Thompson et al. 1997; Aerts & Chapin 2000). In contrast, Körner (1989, 2003) found for several mountain areas that plant tissue N and P tended to increase with altitude due to increasing climatic constraints on biomass production. Nevertheless, our leaf nutrient concentration data seem representative for our site, since they are similar to those measured and reported independently by Makarov et al. (1999) for several species of the same site. Also, three widespread species (*Vaccinium vitis-idaea*, *Carex* spp. and *Festuca ovina*) occur in similar investigations at other sites (Rorison 1971; Wielgolaski et al. 1975; Shaver & Lechowicz 1985; Michelsen et al. 1998; Kudo et al. 2001; Güsewell & Koerselman 2002). N-concentrations in all three species and P in *Vaccinium vitis-idaea* are broadly similar to our findings. P in *Festuca ovina* reported for wetlands (Güsewell & Koerselman 2002) is also low (ca. 0.5 $mg.g^{-1}$), but still 2.5 times higher than in our site. However, our P-value was still well above the detection limit of 0.05 $mg.g^{-1}$ for the P-analysis. Plant tissue P can vary substantially between years (Mamolos & Veresoglou 2000). Since our sampling year was relatively cold and rainy this could have reduced P somewhat. The other possible source of imprecision might be that some sampled green leaves of *Festuca ovina* had slightly senesced tips. However, P-concentration in the litter material collected later in the same year for another analysis was 2.5 fold lower ($p < 0.001$) than in the green material.

The N:P mass ratio of 29 for the green foliage in the controls of the alpine tundra community would indicate strong P-limitation according to the threshold of 16 proposed by Koerselman & Meuleman (1996). However, our data show that despite high N:P ratio the vascular plant biomass production of our alpine plant community is N-limited. The high N:P ratio is driven by the extremely low P-concentration. Thus, the community seems to be composed of species well adapted to low phosphorus supply. Such adaptations might include a highly efficient annual internal P-cycling or (and) high P-use efficiency (Aerts & Berendse 1988; Bobbink et al. 1989).

Whilst our leaf nutrient concentration data for individual species mostly correspond with available literature data for similar sites, our data on the relation between foliar N:P ratio and nutrient limitation contrast not only with those for lowlands (Güsewell & Koerselman 2002; Olde Venterink et al. 2003), but also with some mountain studies (Bowman et al. 1993; Tessier & Raynal 2003), which were consistent with the Koerselman & Meuleman (1996) model. One partial explanation might be the high relative biomass of *Festuca ovina* and *Carex* spp. in our site, because P-concentrations are very low in both species. Apparently, both species grow well at low external P-supply.

We are aware that our calculated vascular plant community N:P ratio is only an estimate, because (1) it is based on data for nine species only and (2) we measured only leaf nutrient concentration but excluded stems. While the biomass of vegetative stems is almost negligible, generative stems contribute considerably to above-ground biomass. Foliar N-concentrations are approximately 30% higher than in petioles and stems (Körner 1989), while foliar P-concentrations are approximately 30% lower than in petioles and stems. If generative parts represented 20% of total biomass and had 30% less N but 30% more P than leaves, the N:P ratio would have been 26; if inflorescences represented 40%, the N:P ratio would have been 24. All these values would, however, still indicate P-limitation in the Koerselman & Meuleman (1996) model.

Vascular plant species responses versus community responses

The response of individual vascular plant species to the nutrient treatments differed from the overall community response, possibly indicating competitive interactions between species. Several studies in arctic and alpine plant communities have demonstrated that N- or N+P-fertilization causes strong biomass increases of graminoids (e.g. Henry et al. 1986; Fox 1992; Bowman et al. 1993; van Wijk et al. 2003), which often replace forbs.

Our results, however, show very different responses of the graminoid *Carex* spp. and *Festuca ovina*. While *Carex* strongly increased its biomass in response to addition of N and N+P and did not respond to P-treatments, *Festuca* had an opposite response, increasing biomass strongly in both P-addition treatments. The responses of *Carex* to the N+P and N-treatment were similar, while *Festuca* showed a doubled increase in response to N+P treatment in comparison with that in the P-treatment. These findings are consistent with previous studies, which have shown that *F. ovina* is a stress-tolerant species but a bad competitor on richer soils, where it is easily eliminated by other species (Harper 1971; MacGillivray & Grime 1995; Thompson et al. 1996). Tyler (1996) reported that the abundance of *F. ovina* was positively correlated with the availability of exchangeable soil phosphates. Thus, consistent with the claim by Grime (2001) that graminoids differ in their response to fertilizers, our data suggest that *Carex* and *Festuca* have opposite nutrient constraints. We speculate here that our *Carex* spp. might possess cluster roots for efficient P-uptake, as Grime (2001) reported for *C. flacca*, and Lamont (1993) for several *Carex* spp.

Changes in N- and P-concentrations induced by the treatments indicate that although most of the species are adapted to low phosphorus supply, P is a secondary limiting nutrient for them. The following arguments underpin this. 1. Fertilization by only N or only P had almost no effect on the concentrations of the other nutrient even when the biomass of the species increased, indicating an absence of dilution. Bowman (1994) reported similar results for the alpine tundra on Niwot Ridge, USA, and interpreted such an absence of dilution as possible co-limitation. 2 For all the species except *Vaccinium vitis-idaea*, leaf N at N-fertilized plots were higher than those at N+P-fertilized plots, by 1.3 times on average (although this was not significant in thee species). Similarly, leaf P in P-fertilized plots had an overall tendency to be higher than those in N+P-plots, by about 1.4 times on average. Additional supply of the second nutrient, thus, results in a more complete utilization of both nutrients, presumably to support the higher biomass production or a higher shoot-root ratio.

Recently attempts have been made to determine whether N:P ratios of individual species can serve as predictors of their nutrient limitation (e.g. Güsewell et al. 2003; Tessier & Raynal 2003). Gerdol et al. (2004) found that leaf N:P of two related species, *Vaccinium vitis-idaea* and *Vaccinium myrtillus*, varied significantly among sites with different nutrient availabilities, indicating different nutrient requirements of these species. Güsewell (2003), showed for Dutch fens and dune slacks that a high N:P ratio (> 20) is associated with P-limitation, while lower values could reflect both N- and N+P- or no limitation. However, Bowman et al. (2003) showed that out of three alpine species the N:P ratio was a useful predictor of a limitation type for only one of them. Similarly, our data suggest no obvious association between the N:P ratio of individual species and their response to nutrient additions.

Total vascular plant community nitrogen and phosphorus pool

As expected, the N- and P-addition treatments increased the N- and P-community pools, respectively. However, the patterns of N- and P-accumulation differed among species. The total N-content was significantly enhanced in N-addition treatments for only a few species (Fig. 2), owing to the increase of these species' biomass and to a lesser extent to the increase in N-concentration. This suggests that higher total N-uptake per unit soil area served primarily to support stronger plant growth. Although the values of the total N-contents were similar in the N- and N+P-treatments, the contributions of the various species differed considerably (Table 1). This depended also mostly on shifts in the species' biomasses. In the N-treated plots, *Carex* and non-rhizobial (Onipchenko et al. 2001) *Trifolium polyphyllum* were the strongest N-accumulators. Addition of phosphorus on N+P-treated plots reduced the contribution of *Trifolium* and *Carex* to the N-pool, while the contribution of *Festuca* and *Alchemilla* increased. In contrast, the increase of the total phosphorus pool under the N+P- and especially the P-treatment seemed to be driven rather by the increases in species P-concentration and was therefore distributed more evenly among many species.

Phosphorus concentration under P-treatment was on average 7.4 times higher than in the control, but only in *Festuca ovina* did this coincide with biomass increase, probably indicating 'luxury consumption'. This is possibly a result of the restricted ability of roots to change their P-absorption capacity, typical for species from infertile soils (Chapin 1980). This is consistent with data reported by Shaver & Chapin (1995) who found that, in Alaskan tundra, increases in P were also greater than increases in N at similar fertilization regimes. In Alaskan tundra plant communities, P-addition stimulated the uptake of P much more than it supported biomass increase (Chapin et al. 1978; Kielland & Chapin 1994; Chapin 1995). Our results show similar luxury consumption of P for an alpine tundra. The observed increase of P in the N+P-treatment can be explained by a relative excess amount of supplied P, because the optimal ratio of fertilizer N:P-supply is 10:1, whereas our N+P-addition had a ratio of 3.6:1.

Concluding remarks

The vascular plant biomass production in the investigated Caucasian alpine tundra plant community is limited by nitrogen, while P is a secondary limiting nutrient. The critical N:P mass ratio (16) for the shift between N- and P-limited plant growth as found for lowland wetlands was not valid for this plant community. This may be caused by the presence of many species that are well adapted to low P-supply. Further research is needed on the P-use efficiency and P-resorption of the component species of alpine tundra communities, since currently we can not give an explanation for their ability to grow at such low internal P-concentrations.

Individual species appear to differ in their nutrient constraints and therefore in their specific adaptations to low P versus N. Thus, the observed community response is the combination of many, sometimes opposite, species responses. Assuming that there is smaller-scale heterogeneity in P- versus N-availability of the soil, such differences in response could promote the optimization of nutritional niche utilization.

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References

Aerts, R. & Berendse, F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio* 76: 63-69.

Aerts, R. & Chapin, F.S. III 2000. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30: 1-67.

Bremner, J.M. 1995. Recent research on problems in the use of urea as a nitrogen fertilizer. *Fert. Res.* 42: 321-329.

Bowman, W.D. 1994. Accumulation and use of nitrogen and phosphorus following fertilization in two alpine tundra communities. *Oikos* 70: 261-270.

Bowman, W.D. & Fisk, M.F. 2001. Primary production. In: Bowman, W.D & Seastedt, T. (eds.) *Structure and function of an alpine ecosystem*, pp. 177-197. Oxford University Press, Oxford, UK.

Bobbink, R., den Dubbelden, K. & Willems, J.H. 1989. Seasonal dynamics of phytomass and nutrients in chalk grassland. *Oikos* 55: 216-224.

Bowman, W.D., Theodose, T.A., Schardt, J.C. & Conant, R.T. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74: 2085-2097.

Bowman, W.D., Bahn, L. & Damm, M. 2003. Alpine landscape variation in foliar nitrogen and phosphorus concentrations and the relation to soil nitrogen and phosphorus availability. *Arct. Antarct. Alp. Res.* 35: 144-169.

Chapin, F.S. III 1980. The mineral nutrition of wild plants, *Annu. Rev. Ecol. Syst.* 11: 233-260.

Chapin, F.S. III 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.

Chapin, F.S. III, Barsdate, R.J. & Barél, D. 1978. Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. *Oikos* 31: 189-199.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Gwynn Jones, D., Jonasson, S., Chapin, F.S. III, Molau, U., Neill, C., Lee, J.A., Melillo, J.M., Sveinbjörnsson, B. & Aerts, R. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J. Ecol.* 89: 984-994.

Fox, J.F. 1992. Responses of diversity and growth-form dominance to fertility in Alaskan tundra fellfield communities. *Arct. Alp. Res.* 24: 233-237.

Gerdol, R., Anfodillo, T., Gualmini, M., Cannone, N., Bragazza, L. & Brancaleoni, L. 2004. Biomass distribution of two subalpine dwarf shrubs with contrasting leaf habit in relation to soil moisture and soil nutrient content. *J. Veg. Sci.* 15: 457-464.

Grime, J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties*. John Wiley & Sons, Chichester, UK.

Grishina, L.A., Onipchenko, V.G. & Makarov, M.I. 1986. *Composition and structure of alpine heath biogeocoenosis*. Izdatelstvo Moskovskogo Universiteta, Moscow. (In Russian.)

Güsewell, S. & Koerselman, W. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspect. Plant Ecol. Evol. Syst.* 5: 37-61.

Güsewell, S., Koerselman, W. & Verhoeven, J.T.A. 2003. Biomass N:P ratios as indicators of nutrient limitation for plant populations in wetlands. *Ecol. Appl.* 13: 372-384.

Harper, J.K. 1971. Grazing, fertilizers and pesticides in the management of grasslands. In: Dufley, E. & Watt, A.S. (eds.) *The scientific management of animal and plant communities for conservation*, pp. 15-31. Blackwell Scientific Publications, Oxford, UK.

Henry, G.H.R., Freedman, B. & Svoboda, J. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. *Can. J. Bot.* 64: 2502-2507.

Khutinaev, M.B. 1981. *Effectiveness of mineral fertilisers on mountain grasslands in the central part of the NorthWest Caucasus*. PhD Thesis, Vsesouzny nauchno-issledovatelsky institut kormov, Moscow. (In Russian.)

Kielland, K. & Chapin, F.S. III 1994. Phosphate uptake in arctic plants in relation to phosphate supply: the role of spatial and temporal variability. *Oikos* 70: 443-448.

Koerselman, W. & Meuleman, A.F.M. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33: 1441-1450.

Körner, C. 1989. The nutritional status of plants from high altitudes. *Oecologia* 81: 379-391.

Körner, C. 2003. *Alpine plant life: Functional plant ecology of high mountain ecosystems*. 2nd. ed. Springer, Berlin, DE.

Kudo, G., Molau, U. & Wada, N. 2001. Leaf-trait variation of tundra plants along a climatic gradient: an integration of responses in evergreen and deciduous species. *Arct. Antarct. Alp. Res.* 33: 181-190.

Lamont, B.B. 1993. Why are hairy root clusters so abundant in the most nutrient-impoverished soils of Australia? *Plant Soil* 155/156: 269-272.

MacGillivray, C.W., Grime, J.P. & The Integrated Screening Programme (ISP) Team 1995. Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Funct. Ecol.* 9: 640-649.

Makarov, M.I., Onipchenko, V.G., Malysheva, T.I., Bulatnikova, I.V. & Vertelina, O.S. 1999. Biological cycle and role of plants in the formation of certain soil properties in alpine ecosystems in North-west Caucasus area. *Vestn. Mosk. Univ., seria, 17, Pochvovedenie* 3: 29-37. (In Russian with English summary.)

Mamolos, A.P. & Veresoglou, D.S. 2000. Patterns of root activity and responses of species to nutrients in vegetation of fertile alluvial soil. *Plant Ecol.* 148: 245-253.

Michelsen, A., Quarmby, C., Sleep, D. & Jonasson, S. 1998. Vascular plant ^{15}N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* 115: 406-418.

Murphy, J. & Riley, J.P. 1962. A modified single solution method for determination of phosphate in natural waters. *Anal. Chim. Acta* 27: 31-36.

Nakhutsrishvili, G.S. 1976. Ecological research on Kazbegi mountain research station. *Ecologia* 3: 81-86 (In Russian.)

Olde Venterink, H., Wassen, M.J., Verkroost, A.W.M. & Ruiter, P.C. 2003. Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* 84: 2191-2199.

Onipchenko, V.G. 1994. Study area and general descriptions of the investigated communities. In: Onipchenko, V.G. & Blinnikov, M.S. (eds.) *Experimental investigation of alpine plant communities in the Northwestern Caucasus*, pp. 6-22. Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel Zür. 115.

Onipchenko, V.G. 2002. *Alpine vegetation of the Teberda Reserve, the Northwestern Caucasus*. Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel, Zür. 130.

Onipchenko, V.G., Makarov, M.I. & van der Maarel, E. 2001. Influence of alpine plants on soil nutrient concentrations in a monoculture experiment. *Folia Geobot.* 36: 225-241.

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V. & Lee, J.A. 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. *J Ecol.* 86: 315-327.

Rorison, I.H. 1971. The use of nutrients in the control of the floristic composition of grassland. In: Dufley, E. & Watt, A.S. (eds.) *The scientific management of animal and plant communities for conservation,* pp. 65-77. Blackwell Scientific Publications, Oxford, UK.

Rorison, I.H. 1980. The effects of soil acidity on nutrient availability and plant response. In: Hutchinson, T.C. & Havas, M. (eds.) *The effect of acid precipitation on terrestrial ecosystems,* pp. 283-304. Plenum Publ. Corp., New York, NY, US.

Shatvorjan, P.V. 1960. Influence of mineral fertilisers on productivity of alpine pastures. *Tr. Armyanskogo nauch.-issled. inst. Zhivotnovodstva i Veterinarii* 4: 191-197 (In Russian.)

Shaver, G.R. & Chapin F.S. III 1995. Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* 18: 259-275.

Shaver, G.R. & Lechowicz, M.J. 1985. A multivariate approach to plant mineral nutrition: dose - response relations and nutrient dominance in factorial experiments. *Can. J. Bot.* 63: 2138-2143.

Tessier, J.T. & Raynal, D.J. 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J. Appl. Ecol.* 40: 523-534.

Thompson, K., Hillier, S.H., Grime, J.P., Bossard, C.C. & Band, S.R. 1996. A functional analysis of a limestone grassland community. *J. Veg. Sci.* 7: 371-380.

Thompson, K., Parkinson, J.A., Band, S.R. & Spencer, R.E. 1997. A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytol.* 136: 679-689.

Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M. & Roelofs, J.G.M. 2004 Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? *J. Appl. Ecol.* 41: 139-150.

Tyler, G. 1996. Cover distributions of vascular plants in relation to soil chemistry and soil depth in a granite rock ecosystem. *Vegetatio* 127: 215-223.

van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S. III, Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, J., Lee, J.A., Michelsen, A., Press, M.C. Richardson, R.H. & Rueth, H. 2003. Long – term ecosystem level experiments at Toolik Lake, Alaska and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biol.* 10: 105-123.

von Liebig, J. 1840. *Chemistry in its application to agriculture and physiology*. Taylor and Walton, London, UK.

Vorob'eva, F.M. & Onipchenko, V.G. 2001. Vascular plants of the Teberda Reserve. *Flora i fauna zapovednikov* 99: 1-100. (In Russian.)

Wielgolaski, F.E. 1972. Vegetation types and primary production in tundra. In: Wielgolaski. F.E. & Rosswall, T. (eds.) *Tundra Biome, Proceedings IV. International Meeting on the Biological Production of Tundra, Leningrad 1971*, pp. 9-34. Tundra Biome Steering Committee, Stockholm, SE.

Wielgolaski, F.E., Kjevik, S. & Kallio, P. 1975. Mineral content of tundra and forest tundra plants in Fennoscandia. In: Wielgolaski, F.E. (ed.) *Fennoscandian tundra ecosystems. Part 1. Plants and microorganisms*, pp. 316-332. Springer-Verlag, Berlin, DE.

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